The Journal of Experimental Biology 207, 1771-1778
Published by The Company of Biologists 2004
doi:10.1242/jeb.00946

Navigation and seasonal migratory orientation in juvenile sea turtles

Larisa Avens[1,2,*] and Kenneth J. Lohmann[1]
[1]*Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, USA* and [2]*NOAA Fisheries, Beaufort, NC 28516-9722, USA*
*Author for correspondence (e-mail: larisa.avens@noaa.gov)

Accepted 17 February 2004

Summary

Juvenile loggerhead and green turtles that inhabit inshore waters of North Carolina, USA undertake long seasonal migrations, after which they often return to specific feeding areas. In addition, juvenile turtles are capable of homing to specific sites after being displaced. As a first step towards investigating the navigational mechanisms that underlie these movements, juvenile turtles were captured in coastal waters of North Carolina and displaced 30–167 km along circuitous routes while deprived of visual cues. At the testing location, turtles were tethered in a circular arena and permitted to swim while their orientation was monitored. Between May and September, when juvenile loggerhead and green turtles inhabit feeding areas along the North Carolina coast, turtles oriented in directions that corresponded closely with the most direct route back to their capture locations. During October and November, however, both loggerhead and green turtles oriented southward, a direction consistent with the migratory paths of turtles beginning their autumn migration. The results demonstrate for the first time that both homing and migratory orientation can be elicited in juvenile turtles under laboratory conditions in which orientation cues can be readily manipulated. In addition, the results provide evidence that juvenile loggerheads can assess their position relative to a goal using local cues available at the test site and are therefore capable of map-based navigation.

Key words: sea turtle, orientation, navigation, migration, map, loggerhead, green turtle, *Caretta caretta*, *Chelonia mydas.*

Introduction

After a period of years spent in the pelagic environment, juvenile loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles originating from natal beaches along the east coast of the USA take up residence in inshore waters such as sounds, bays and estuaries (reviewed by Musick and Limpus, 1997; Hopkins-Murphy et al., 2003). Juveniles of both turtle species appear to inhabit limited home ranges (Mendonca and Ehrhart, 1982; Mendonca, 1983; Byles, 1988) and often exhibit homing behavior, returning to specific sites after displacements (Ireland, 1980; Ryder, 1995; Musick and Limpus, 1997; Avens et al., 2003).

Loggerheads and green turtles that occupy temperate and sub-tropical regions often undertake seasonal migrations, presumably to avoid lethal water temperatures that occur during winter months (Morreale et al., 1992; Shoop and Kenney, 1992; Epperly et al., 1995a,b). For example, turtles from inshore waters in North Carolina, Virginia and New York migrate south/southeast during autumn months to reach warmer, coastal waters or the Gulf Stream (Shoop and Kenney, 1992; Keinath, 1993; Morreale and Standora, 1995; NOAA Beaufort Laboratory, unpublished data). In the spring, some of these juveniles migrate back to the same specific northern feeding sites that they inhabited during the warm months of the previous year (Byles, 1988; Avens et al., 2003).

Little is known about the mechanisms of orientation and navigation that enable juvenile and adult sea turtles to navigate to specific targets, such as feeding areas, or to complete long, seasonal migrations. The guidance mechanisms of hatchling turtles have been studied extensively (reviewed by Lohmann et al., 1997; Lohmann and Lohmann, 2003), but ontogenetic changes in orientation and navigation are known to occur in many animals (Wiltschko, 1983; Baker, 1984; Able and Bingman, 1987; Rodda and Phillips, 1992; Able and Able, 1996). Thus, the strategies and mechanisms used by large, juvenile turtles, as well as by adults, may differ significantly from those used by hatchlings beginning their first migration.

As a first step towards investigating mechanisms of orientation and navigation in older turtles, we have adapted techniques used to study hatchlings for use with juvenile turtles captured in inshore waters. The results indicate that both homing behavior and seasonal migratory orientation can be elicited in an experimental arena under conditions in which environmental variables can be carefully controlled. In addition, the results provide strong evidence that juvenile turtles can assess their position relative to a destination using cues available at the test site and are therefore capable of map-based navigation.

Materials and methods

Experimental animals

Juvenile loggerhead (*Caretta caretta* L.) and green (*Chelonia mydas* L.) turtles were captured in the coastal waters of North Carolina, USA. Most animals used in this study were incidentally captured in pound nets set by fishermen in Core Sound and southern Pamlico Sound (Fig. 1). Although turtles were caught in Core Sound during the summer and autumn, they were only obtained from Pamlico Sound during the autumn because pound nets are only fished there during that time of year. A limited number of turtles was also obtained from areas outside of Core and Pamlico Sounds (Fig. 1). All animals obtained from these other areas were loggerheads that were incidentally captured in gill nets, skimmer trawls or in the cooling water intake canal at the Carolina Power & Light Nuclear Power plant in Brunswick Co., North Carolina. Juvenile loggerheads measuring 42.3–70.4 cm standard straight-line carapace length (SCL) and juvenile green turtles measuring 21.2–44.0 cm SCL were retained for experiments. Each turtle was tagged to ensure that no turtle was tested more than once.

Although specific age estimates are not available for the turtles used in this study, current estimates of pelagic stage duration for loggerheads recruiting to the benthic environment at 46–64 cm SCL range from 7.0 to 11.5 years (Bjorndal et al., 2003). Thus, the majority of loggerheads used for these experiments were probably at least 7 years old. Estimates of ages for juvenile green turtles inhabiting inshore waters in Florida range from 2 years at 21 cm to 7 years at 44 cm, indicating that the green turtles obtained for our study were at least 2 years of age (Zug and Glor, 1998).

All turtles were first transported by boat to land and then by vehicle to the testing site at the National Oceanic and Atmospheric Administration (NOAA) Laboratory in Beaufort, North Carolina (Fig. 1). Turtles caught during fishing operations were typically held in the boat for ~1–3 h before being taken to shore. During this time, turtles were prevented from viewing their surroundings and the sky, and the boat moved along indirect, circuitous routes that typically involved multiple detours to different fishing nets. Loggerheads captured at the nuclear power plant intake canal were transported uncovered, first by boat and then in a truck, to a temporary holding facility approximately 2 km away, where they were held for less than 6 h before being transported to the NOAA lab. All overland transport to the lab occurred during daylight hours. During these trips, turtles from all capture sites were kept inside the vehicle, where they were unable to view their surroundings, and transported to the test site by indirect routes along winding coastal roads. The test site was approximately 30 km (straight-line distance) from capture

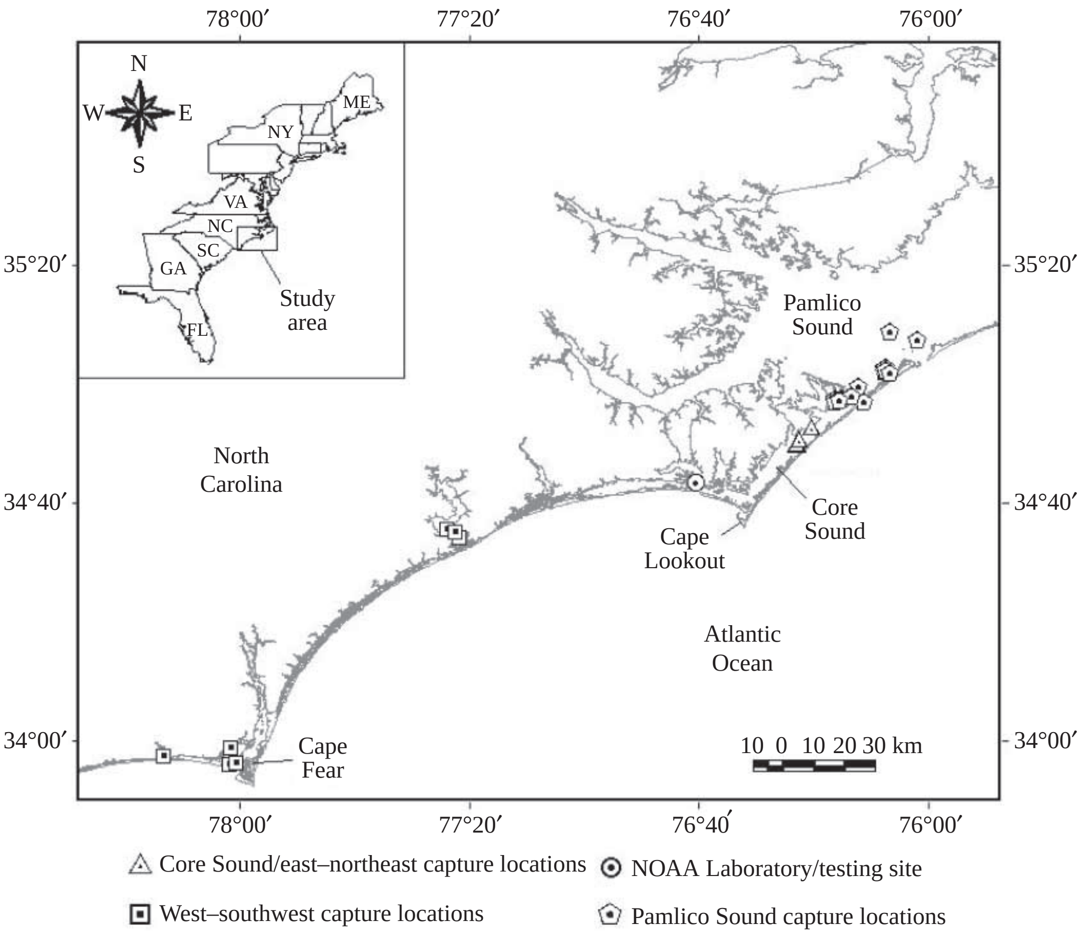


Fig. 1. Map of the coastal areas of North Carolina indicating the location of the testing site (NOAA Laboratory) and the locations where turtles were captured.

locations in Core Sound, 45–74 km from capture sites in Pamlico Sound and 65–167 km from capture areas outside of Core and Pamlico Sounds.

At the laboratory, each turtle was placed into an outdoor, circular, holding tank measuring 2 m in diameter that was partially covered to provide shade. The walls of each tank blocked the view of the horizon and any natural landmarks; however, turtles were able to view the sky directly above and might have glimpsed the tops of nearby buildings and trees. Sea water was continuously circulated through the tanks and water depth was maintained at 0.75 m. Turtles were allowed to acclimate to captive conditions for approximately 24 h before being used in experiments.

Orientation arena and data acquisition

Juvenile turtles were tested in an experimental arena (Fig. 2) consisting of a circular, fiberglass tank that was 6 m in diameter and 1.5 m high (Red Ewald, Karnes City, TX, USA). The arena, which was filled with seawater to a depth of 0.75 m, was located outdoors and was uncovered, allowing the turtles to view the sky. However, the walls of the tank blocked the turtles' view of the natural horizon and surroundings.

During testing, each turtle was outfitted with a nylon–Lycra™ harness that encircled the carapace. The turtle was then tethered to a rotatable arm mounted at the center of the arena (Fig. 2). As the turtle swam, the tether pulled the arm so that the arm tracked the turtle's swimming direction continuously. A digital encoder coupled to the arm was wired to a nearby computer so that headings could be recorded to the nearest 1.4° at intervals of 30 s.

Immediately before and after each trial, the tracking system was checked to ensure that data were recorded accurately relative to magnetic north (0°). In addition, the water was stirred prior to each trial to ensure that no chemical gradients existed in the tank.

Testing procedure

All experiments were conducted between May and November, months when turtles inhabit coastal waters of North Carolina or migrate through them (Epperly et al., 1995a,b). Trials were conducted during daylight hours, between 12:30 h and 17:00 h, under diverse weather conditions.

To minimize the possibility that the orientation of a turtle upon release might influence the direction it subsequently swam, green turtles were released in the center of the arena facing random directions. To release loggerheads (which were much larger and heavier than the green turtles), it was necessary to stand on a low platform, which was located just outside the northern edge of the arena. Thus, all loggerheads were released in the north, but successive animals were released facing east and west.

After a turtle was tethered to the arm and released in the tank, it was allowed a 5-min acclimation period before the trial was initiated. The data acquisition computer then recorded the turtle's directional headings for the next 10 min, resulting in 20 measurements of headings. At the end of the 10-min trial, the computer calculated a mean angle on the basis of the 20 data points. This angle represented the average direction that the turtle swam (Batschelet, 1981).

Trials were observed from a raised platform located approximately 5 m from the perimeter of the tank. Previous tests have demonstrated that the presence of observers at this distance does not influence the orientation of turtles swimming in the arena (Avens and Lohmann, 2003). These observations are consistent with similar findings involving hatchling turtles (Salmon and Lohmann, 1989; Witherington, 1991). Animals were monitored to ensure that they swam consistently at the end of the tether. Turtles were eliminated from the study if, during three or more computer readings, they either did not swim (i.e. they floated motionless or sat on the bottom of the tank) or they moved backwards or otherwise swam erratically so that the direction of the rotatable arm did not accurately reflect the turtle's orientation.

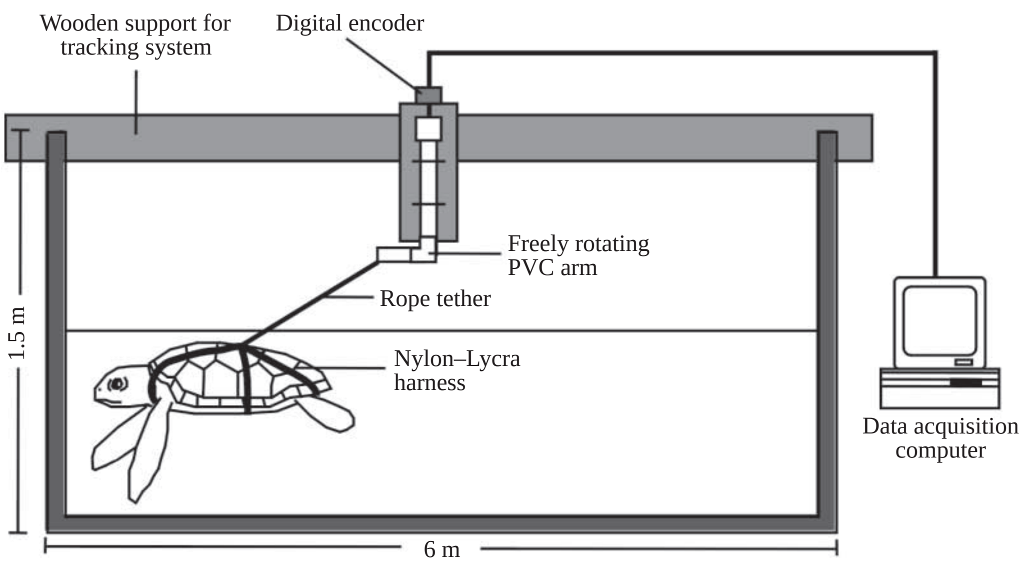


Fig. 2. Diagram of the experimental arena and the data acquisition system used to monitor the orientation of juvenile sea turtles (turtle not drawn to scale). Each turtle was outfitted with a nylon–Lycra™ harness and tethered to a rotatable arm in the arena. The data acquisition computer was located in a shed approximately 5 m to the south of the arena. See text for details.

Data analysis

In North Carolina, sea turtles occupy inshore waters from approximately April through September and begin to migrate when water temperatures decrease during October and November (Epperly et al., 1995a). Data obtained between May and September ('summer') were therefore analyzed to determine whether turtles exhibited orientation that might represent homing to the feeding areas where they were captured. By contrast, data collected during October and November ('autumn') were analyzed to determine whether turtles exhibited seasonally appropriate migratory orientation. Because turtles were obtained from Pamlico Sound only during the autumn, no data for turtles caught in this area were used in the homing analysis.

The distributions of headings for turtles tested during the summer were analyzed using the *V*-test in conjunction with the 95% confidence interval for the mean angle. This was done to determine whether turtles in each group were significantly oriented in a direction that was consistent with the direction of their capture location (Batschelet, 1981). The 'homeward' direction for loggerhead and green turtles captured in Core Sound, to the east–northeast of the testing site, was 74°. Because loggerheads obtained to the west–southwest of the testing site were caught at several different locations (Fig. 1), a mean homeward bearing (255°) was calculated for these turtles and this bearing was used for the *V*-test analysis. Watson's U^2 test was used to determine whether the headings of loggerheads obtained to the east–northeast and to the west–southwest were significantly different (Batschelet, 1981).

Data obtained from turtles tested during the autumn were analyzed using the Rayleigh test to determine whether the turtles were significantly oriented (Batschelet, 1981). The *V*-test was not used in this case because the precise direction of the migration (e.g. south *vs* southeast) could not be predicted. Watson's U^2 test was used to determine whether the orientation of loggerhead and green turtles in the autumn was significantly different from that observed for each species during the summer (Batschelet, 1981).

Results

Summer orientation

During trials conducted between May and September ('summer'), juvenile loggerheads captured to the east–northeast of the testing site were significantly oriented in a direction that corresponded closely with the most direct path back to their capture area (mean angle=83°, $P<0.0005$, *V*-test, 95% confidence interval ±25°; Fig. 3A). Loggerheads captured to the west–southwest of the testing site during the summer were also significantly oriented, but with a mean heading consistent with the direction of their capture locations (mean angle=271°, $P<0.05$, *V*-test, 95% confidence interval ±76°; Fig. 3B). The two distributions are significantly different ($P<0.001$, Watson's U^2 test).

Juvenile green turtles obtained to the east–northeast during the summer were also significantly oriented towards their capture area (mean angle=50°, $P<0.0025$, *V*-test, 95% confidence interval ±37°; Fig. 4A).

Autumn orientation

Juvenile loggerheads captured east–northeast of the testing site during October and November ('autumn') were significantly oriented with a mean heading of 190° ($P<0.005$; Rayleigh test, 95% confidence interval ±33°; Fig. 3C). This direction of orientation was significantly different from that observed for loggerheads captured to the east–northeast and tested during the summer ($P<0.001$, Watson's U^2 test). Similarly, green turtles tested during the autumn were significantly oriented with a mean heading of 199° ($P<0.02$; Rayleigh test, 95% confidence interval ±39°; Fig. 4B). The orientation of green turtles during summer months differed significantly from orientation during autumn ($P<0.02$; Watson's U^2 test).

Discussion

Homing behavior

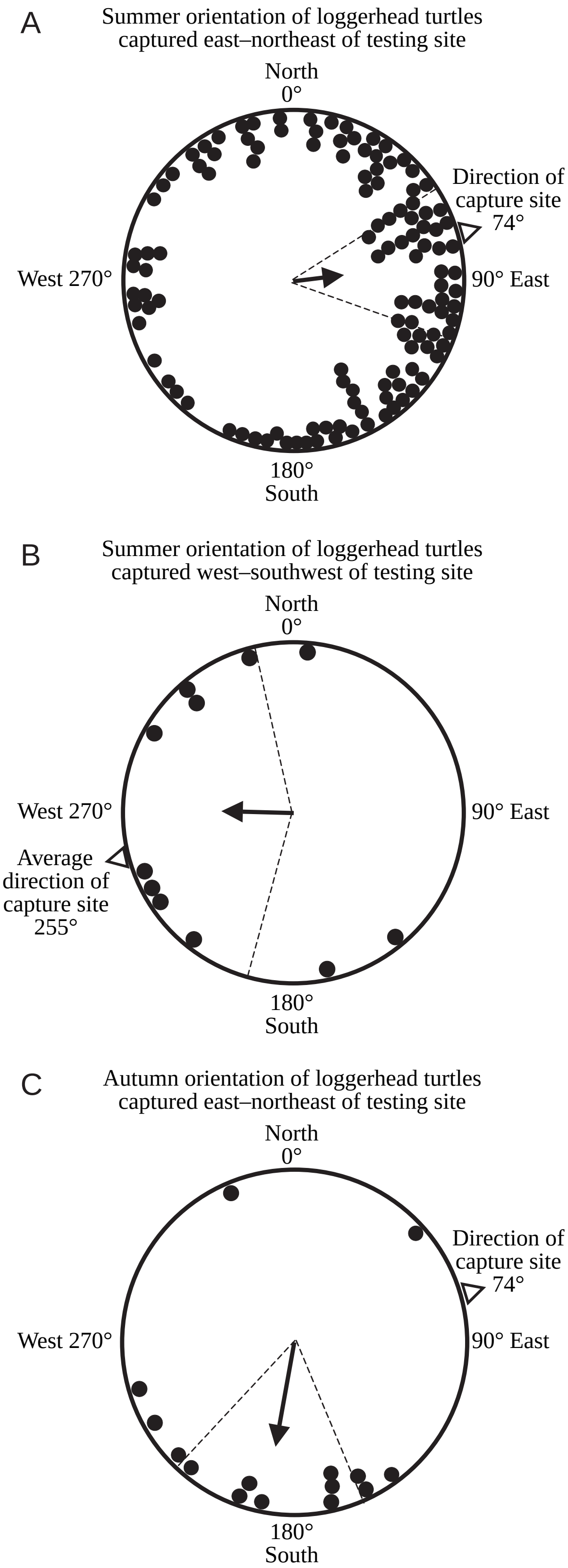
Juvenile loggerheads obtained from areas to the east–northeast and to the west–southwest of the testing site oriented towards their respective capture locations when tested during summer months (Fig. 3A,B). These results imply that the turtles were capable of determining the direction of their capture site, or their 'homeward' direction, after being passively displaced 30–167 km and placed into an orientation arena. These results demonstrate for the first time that homing behavior in sea turtles can be elicited under laboratory conditions in which potential cues can be carefully controlled.

Animals capable of homing are thought to possess both a positional sense to determine geographic location (or at least the direction to the goal) and a directional or compass sense to maintain a heading towards the appropriate homeward direction (Kramer, 1961; Able, 2001). Sea turtles are known to have a magnetic compass sense (Lohmann, 1991; Lohmann and Lohmann, 1996a), and results of recent experiments have provided evidence that juvenile turtles possess a second mechanism for maintaining headings, possibly based on a sun compass or on patterns of skylight polarization (Avens and Lohmann, 2003).

By contrast, little is known about the position-finding system of juvenile and adult sea turtles. In principle, displaced turtles in our experiments might have determined the direction to the capture site in at least two different ways: by monitoring the outward path to the test site or by detecting positional cues available at the test site.

Map-based navigation

One possibility is that the turtles monitored the outward journey to the test site with sufficient resolution to set a course back towards the capture area. However, most turtles remained on fishing boats for at least 1–3 h after capture, during which time the turtles were deprived of visual cues and the boat changed direction and location almost continuously. Turtles were then transported by vehicle for an additional period of ~30–200 min along winding, circuitous routes to the test site.



Thus, to determine the direction towards the capture site using information obtained during the outward journey, turtles would have had to monitor closely the direction and distance of different parts of the trip over both water and land for a period of several hours, in the absence of visual cues, and with little or no information about the velocity of the boat or vehicles. Although such a possibility cannot be excluded with certainty, we consider it unlikely.

An alternative explanation is that turtles determined their position relative to the capture area, or at least the general direction towards the capture area, using cues available at the testing location. Such an ability is known to exist in several animals, including birds (Wiltschko and Wiltschko, 2003), amphibians (Phillips, 1995) and lobsters (Boles and Lohmann, 2003). Our data suggest that sea turtles also possess this ability and are therefore capable of map-based navigation as defined by Able (2001).

The cue or cues that turtles used to assess their position relative to the capture site cannot be determined from these initial experiments. Visual landmarks could not have provided the basis for the positional assessment because no natural landmarks were available in the test arena or holding tanks. Among several potential sources of positional information are location-specific chemical cues (Grassman et al., 1984), if such cues existed in the water in which the turtles were tested, and information from the Earth's magnetic field (Lohmann and Lohmann, 1994, 1996b; Lohmann et al., 2001). Although positional information is also potentially available from celestial cues such as the elevation (height above the horizon) of the sun at specific times of the day, there is presently no evidence that any animal exploits this information in navigation (Gould, 1998).

Homing in the ocean

In several previous studies, juvenile or adult sea turtles were

Fig. 3. Summer and autumn orientation of juvenile loggerhead turtles. Each dot within a circular diagram represents the mean angle of orientation for a single turtle during its 10-min trial. Triangles on the outsides of the circles correspond to the most direct routes back to the capture areas for each group of turtles. The broken lines represent the 95% confidence interval for the mean heading. (A) Orientation of loggerheads captured at locations east–northeast of the test site and tested between May and September 1998–2001. Turtles were significantly oriented with a mean angle of 83° (N=122, r=0.29, P<0.0005 V-test, 95% confidence interval ±25°). The confidence interval overlaps the direction to the capture area (74°). (B) Orientation of loggerheads captured at locations west–southwest of the test site and tested between May and September 1999–2002. Turtles were significantly oriented with a mean angle of 271° (N=11, r=0.43, P<0.05 V-test, 95% confidence interval ±76°). The confidence interval overlaps the direction to the capture site (255°). (C) Autumn orientation of loggerheads tested in October and November 1998–2000. Turtles were significantly oriented with a mean angle of 190° (N=15, r=0.61, P<0.005 Rayleigh test, 95% confidence interval ±33°). This direction coincides with the direction of orientation exhibited by wild turtles during their autumn migration.

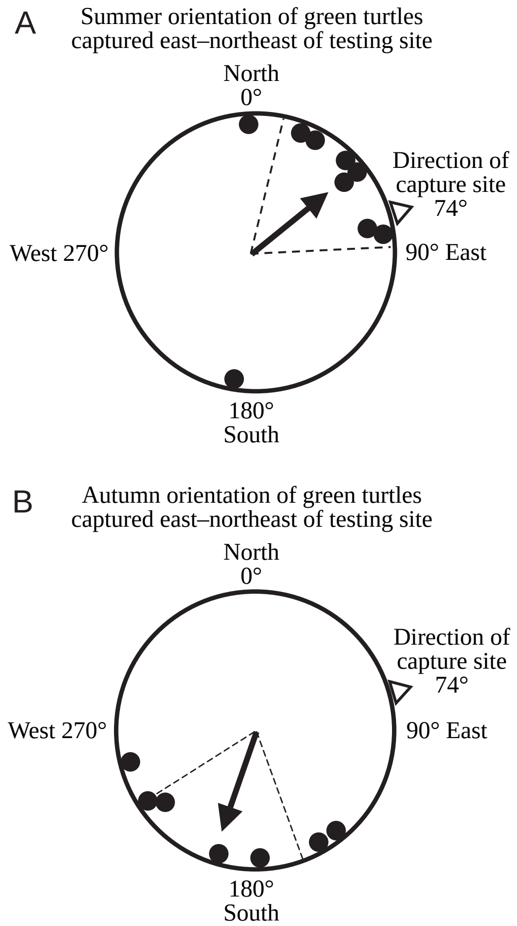


Fig. 4. Summer and autumn orientation of juvenile green turtles. Each dot within a circular diagram represents the mean angle of orientation for a single turtle during its 10-min trial. The triangle on the outside of each circle corresponds to the direction towards the capture area for each group of turtles. The broken lines represent the 95% confidence interval for the mean angle. (A) Orientation of green turtles tested between May and September 1998–1999. Turtles were significantly oriented with a mean angle of 50° (N=9, r=0.71, P<0.0025 V-test, 95% confidence interval ±37°). The confidence interval overlaps the direction to the capture site (74°). (B) Autumn orientation of green turtles tested in October and November 1998 and 2001. Turtles were significantly oriented with a mean angle of 199° (N=7, r=0.76, P<0.02 Rayleigh test, 95% confidence interval ±39°). This direction of orientation is consistent with that observed in wild turtles during the autumn migration.

displaced and released at various distances away from capture sites (Ireland, 1980; Murphy and Hopkins-Murphy, 1990; Ryder, 1995; Standora et al., 1995; Avens et al., 2003). In each case, many returned to the capture area, implying that the turtles have navigational mechanisms that enable them to compensate for displacements and to home to specific locations. These findings are consistent with the observations of Carr (1967), who reported that turtles displaced approximately 50 km from feeding grounds in the Gulf of Mexico often returned rapidly to the sites where they had been captured. They are also consistent with several published anecdotes in which marked turtles displaced from Nicaragua to Florida (Carr, 1956), from Nicaragua to the Cayman Islands (Carr, 1956), and from Ascension Island to the English Channel (Cornelius, 1865) also returned to their original capture sites.

Not all turtle displacements have resulted in clear homing behavior (Luschi et al., 2001, 2003). In general, however, studies in which little or no homing has been reported have involved unusually long displacements, displacement of nesting turtles during the internesting interval when turtles are normally inactive, or placement of satellite transmitters directly on the turtles' heads (Luschi et al., 2001). Because transmitters produce magnetic fields, this last treatment may impair the turtles' ability to perceive magnetic information in the same way that magnets placed on turtles disrupt magnetic orientation (Avens and Lohmann, 2003; Irwin and Lohmann, 2003; Grocott, 2003). Regardless of these considerations, however, our results are consistent with the hypothesis that turtles are capable of map-based navigation.

Migratory orientation

Whereas turtles tested during summer months oriented in directions that coincided with routes towards their capture areas (Figs 3A,B, 4A), turtles tested during the autumn migration oriented southward (Figs 3C, 4B), a direction consistent with the seasonal movements of North Carolina turtles at this time of year (Shoop and Kenney, 1992; Keinath, 1993; Morreale and Standora, 1995; NOAA Beaufort Laboratory, unpublished data). These results demonstrate for the first time that seasonal migratory orientation can be elicited in juvenile loggerhead and green turtles under controlled conditions.

The orientation behavior of the turtles during the migratory season closely parallels the restlessness exhibited by captive, migratory birds (Wiltschko and Wiltschko, 1991). Avian researchers have been able to exploit this behavior to investigate a number of factors related to bird migration, including the cues used to orient and navigate (Munro et al., 1997; Wiltschko et al., 1998), the genetic basis of migratory orientation (Helbig, 1996; Pulido et al., 2001) and the circannual rhythms involved in migration (Gwinner, 1996). Similar topics can now be studied in sea turtles using the techniques described in this study.

We are grateful for assistance provided by S. Epperly, J. McNeill, J. Keller, J. Weaver, K. Hart, C. Taylor and the many volunteers and fishermen who participated in turtle capture, particularly Dave Beresoff, Timmy Edens and George Baird. We thank the National Aquarium in Baltimore for providing the circular tank used as an orientation arena and the staff of the NOAA Beaufort Laboratory for logistical support. The manuscript was improved by critiques provided by C. Taylor, M. Baltzley, L. Boles, W. P. Irwin, C. M. F. Lohmann, C. Mora and J. Wang. We gratefully acknowledge financial support from the National Marine Fisheries Service, the PADI Foundation, PADI Project AWARE, Lerner-Grey

Fund for Marine Research, Sigma-Xi, the University of North Carolina – Chapel Hill Wilson Fund, and the National Science Foundation (grant IBN-9816065). Research on endangered sea turtles was authorized by NMFS Scientific Research Permit #1260 and USFWS Permit #TE-676379-2.

References

Able, K. P. (2001). The concepts and terminology of bird navigation. *J. Avian Biol.* **32**, 174-183.

Able, K. P. and Able, M. A. (1996). The flexible migratory orientation system of the Savannah sparrow (*Passerculus sandwichensis*). *J. Exp. Biol.* **199**, 3-8.

Able, K. P. and Bingman, V. P. (1987). The development of orientation and navigation behavior in birds. *Q. Rev. Biol.* **62**, 1-29.

Avens, L. and Lohmann, K. J. (2003). Use of multiple orientation cues by juvenile loggerhead sea turtles (*Caretta caretta*). *J. Exp. Biol.* **206**, 4317-4325.

Avens, L., Braun, J. B., Epperly, S. P. and Lohmann, K. J. (2003). Site fidelity and homing behavior in juvenile loggerhead sea turtles, *Caretta caretta*. *Mar. Biol.* **143**, 211-220.

Baker, R. R. (1984). *Bird Navigation: The Solution of a Mystery?* London: Hodder & Stoughton.

Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.

Bjorndal, K. A., Bolten, A. B., Dellinger, T., Delgado, C. and Martins, H. (2003). Compensatory growth in oceanic loggerhead sea turtles: response to a stochastic environment. *Ecology* **84**, 1237-1249.

Boles, L. C. and Lohmann, K. J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60-63.

Byles, R. (1988). Behavior and ecology of sea turtles from Chesapeake Bay, Virginia. *Ph.D. Dissertation.* College of William and Mary, Williamsburg, VA, USA.

Carr, A. (1956). *The Windward Road*. New York: Alfred Knopf, Inc.

Carr, A. (1967). *So Excellent a Fishe*. New York: The Natural History Press.

Cornelius, C. (1865). *Die Zug- und Wander-Thiere aller Thierclassen.* Berlin: J. Springer.

Epperly, S. P., Braun, J. and Veishlow, A. (1995a). Sea turtles in North Carolina waters. *Conserv. Biol.* **9**, 384-394.

Epperly, S. P., Braun, J. and Chester, A. J. (1995b). Aerial surveys for sea turtles in North Carolina inshore waters. *Fish. Bull.* **93**, 254-261.

Gould, J. L. (1998). Sensory bases of navigation. *Curr. Biol.* **8**, R731-R738.

Grassman, M. A., Owens, D. W., McVey, J. P. and Marquez, R. M. (1984). Olfactory-based orientation in artificially imprinted sea turtles. *Science* **224**, 83-84.

Grocott, P. (2003). Turn turtle turn. *Navigation News* **Sept./Oct.**, 11-12.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39-48.

Helbig, A. (1996). Genetic basis, mode of inheritance and evolutionary changes of migratory directions in Palearctic warblers (Aves: Sylviidae). *J. Exp. Biol.* **199**, 49-55.

Hopkins-Murphy, S. R., Owens, D. W. and Murphy, T. M. (2003). Ecology of immature loggerheads on foraging grounds and adults in internesting habitat in the eastern United States. In *Loggerhead Sea Turtles* (ed. A. Bolten and B. Witherington), pp. 79-92. Washington, DC: Smithsonian Institution Press.

Ireland, L. C. (1980). Homing behavior of juvenile green turtles, *Chelonia mydas*. In *A Handbook for Biotelemetry and Radio Tracking* (ed. J. Amlaner and D. S. MacDonald), pp. 761-764. Oxford: Pergamon Press.

Irwin, W. P. and Lohmann, K. J. (2003). Magnetic-induced disorientation in hatchling loggerhead sea turtles. *J. Exp. Biol.* **206**, 497-501.

Keinath, J. A. (1993). Movements and behavior of wild and head-started sea turtles. *Ph.D. Dissertation.* College of William and Mary, Williamsburg, VA, USA.

Kramer, G. (1961). Long-distance orientation. In *Biology and Comparative Physiology of Birds* (ed. A. J. Marshall), pp. 341-371. New York: Academic Press.

Lohmann, K. J. (1991). Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *J. Exp. Biol.* **155**, 37-49.

Lohmann, K. J. and Lohmann, C. M. F. (1994). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23-32.

Lohmann, K. J. and Lohmann, C. M. F. (1996a). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73-81.

Lohmann, K. J. and Lohmann, C. M. F. (1996b). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59-61.

Lohmann, K. J. and Lohmann, C. M. F. (2003). Orientation mechanisms of hatchling loggerheads. In *Loggerhead Sea Turtles* (ed. A. Bolten and B. Witherington), pp. 44-62. Washington, DC: Smithsonian Institution Press.

Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. F. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366.

Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F. and Salmon, M. (1997). Orientation, navigation, and natal beach homing in sea turtles. In *The Biology of Sea Turtles* (ed. P. Lutz and J. Musick), pp. 107-136. Boca Raton: CRC Press.

Luschi, P., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Hays, G. C. (2001). Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behav. Ecol. Sociobiol.* **50**, 528-534.

Luschi, P., Hughes, G. R., Mencacci, R., De Bernardi, E., Sale, A., Broker, R., Bouwer, M. and Papi, F. (2003). Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open ocean. *Mar. Biol.* **143**, 793-801.

Mendonca, M. T. (1983). Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia* **1983**, 1013-1023.

Mendonca, M. T. and Ehrhart, L. M. (1982). Activity, population size, and structure of immature *Chelonia mydas* and *Caretta caretta* in Mosquito Lagoon, Florida. *Copeia* **1982**, 161-167.

Morreale, S. J. and Standora, E. A. (1995). Cumulative evidence of southward migration of juvenile sea turtles from temperate northeastern waters. *NOAA Technical Memorandum NMFS-SEFSC-36*. Miami, FL: National Marine Fisheries Service.

Morreale, S. J., Meylan, A. B., Sadove, S. S. and Standora, E. A. (1992). Annual occurrence and winter mortality of marine turtles in New York waters. *J. Herpetol.* **26**, 301-308.

Munro, U., Munro, J. A., Phillips, J. B., Wiltschko, R. and Wiltschko, W. (1997). Evidence for a magnetite-based navigational "map" in birds. *Naturwissenschaften*, **84**, 26-28.

Murphy, T. M. and Hopkins-Murphy, S. T. (1990). Homing of translocated gravid loggerhead turtles. In *Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-278* (compilers: T. H. Richardson, J. Richardson and M. Donnelly), pp. 123-124.

Musick, J. A. and Limpus, C. J. (1997). Habitat utilization and migration in juvenile sea turtles. In *The Biology of Sea Turtles* (ed. P. Lutz and J. A. Musick), pp. 137-163. New York: CRC Press.

Phillips, J. B., Adler, K. and Borland, S. C. (1995). True navigation by an amphibian. *Anim. Behav.* **50**, 855-858.

Pulido, F., Berthold, P., Mohr, G. and Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. Lond. B* **268**, 953-959.

Rodda, G. H. and Phillips, J. B. (1992). Navigational systems develop along similar lines in amphibians, reptiles, and birds. *Ethol. Ecol. Evol.* **4**, 43-51.

Ryder, T. S. (1995). Daily movements and relocation of loggerhead turtles (*Caretta caretta*) at Cape Canaveral, Florida. *M.A. Thesis.* State University of New York College at Buffalo, Buffalo, NY, USA.

Salmon, M. and Lohmann, K. J. (1989). Orientation cues used by hatchling loggerhead sea turtles (*Caretta caretta* L.) during their offshore migration. *Ethology* **83**, 215-228.

Shoop, C. R. and Kenney, R. D. (1992). Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. *Herpetol. Monogr.* **6**, 43-67.

Standora, E. A., Eberle, M. D., Edbauer, J. M., Ryder, T. S., Williams, K. L., Morreale, S. J. and Bolten, A. B. (1995). Diving behavior, daily movements, and homing of loggerhead turtles (*Caretta caretta*) at Cape Canaveral, Florida, March and April 1993. In *Sea Turtle Research Program, Summary Report. Final Report. Prepared for US Army Engineer Division, South Atlantic, Atlanta, GA, and US Naval Submarine Base, Kings Bay, GA. Technical Report CERC-95* (compiler: L. Z. Hales), pp. 48-51.

Wiltschko, R. (1983). The ontogeny of orientation in young pigeons. *Comp. Biochem. Physiol. A* **76**, 701-708.

Wiltschko, R. and Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. *Anim. Behav*. **65**, 257-272.

Wiltschko, W. and Wiltschko, R. (1991). Magnetic orientation and celestial cues in migratory orientation. In *Orientation in Birds* (ed. P. Berthold), pp. 17-36. Boston: Birkhauser-Verlag.

Wiltschko, W., Weindler, P. and Wiltschko, R. (1998). Interaction of magnetic and celestial cues in the migratory orientation of passerines. *J. Avian Biol.* **29**, 606-617.

Witherington, B. E. (1991). Orientation of hatchling loggerhead turtles at sea off artificially lighted and dark beaches. *J. Exp. Mar. Biol. Ecol.* **149**, 1-11.

Zug, G. R. and Glor, R. E. (1998). Estimates of age and growth in a population of green sea turtles (*Chelonia mydas*) from the Indian River lagoon system, Florida: a skeletochronological analysis. *Can. J. Zool.* **76**, 1497-1506.